

Diversity and durability: responses of the Madeiran and Porto-Santan snail faunas to natural and human-induced environmental change

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Abstract: The snail fauna of the Madeiran Archipelago has the high regional diversity and endemism, and high species and genus differentiation between islands characteristic of oceanic island faunas. It is unusual in two respects: the existence of good Pleistocene/Holocene fossil records, and the apparent durability of the endemic fauna in the face of massive human disturbance and the introduction of non-indigenous species.

We use the fossil record, the present microdistributions of species, and the environmental records available to track the generation of diversity and the response to human disturbance. The nature of the environment available and the life-habits of endemic species appear to account for the relative resilience of these species.

Land snail faunas of volcanic oceanic islands are usually characterized by very high levels of species diversity and endemism (Solem, 1983, 1984, 1990a). Sample site diversities are not high; there is marked microgeographical differentiation within islands, and evolution at species level occurs mostly within rather than between islands. Overall species diversity in archipelagos is thus often very high indeed (Solem, 1990b).

This situation offers excellent opportunities to study the process of speciation (Clarke and Murray, 1969; Cowie, 1992a) but these are often compromised by the extreme vulnerability of such faunas to habitat destruction and the introduction of predators and competitors (Cowie, 1992b). Thus three-quarters of the endemic fauna of the Hawaiian archipelago is believed to be extinct (Hadfield, 1986; Solem, 1990a, b) and a similar situation occurs on other Pacific islands. Extinction is often very recent: Tomiyama and Kurozumi's (1992) studies on the Ogasawara Islands south of Japan indicate that nearly 40% of endemic species have become extinct since 1945, with higher figures on the most disturbed islands.

Not all oceanic islands have been so drastically affected; the islands of the Gulf of Guinea, retaining some primary forest and lacking introduced predators retain most if not all of their described endemic faunas (Gascoigne, 1994).

While similar in most of these respects to the faunas of other oceanic islands, that of the Madeiran Archipelago differs in that, despite over 500 years of human settlement and disturbance, it has apparently suf-

fered much less. In this paper, we offer an explanation of this robustness, based on analysis of past environmental changes both natural and human-induced. Subfossil, nineteenth-century, and modern records are available as evidence.

Cameron and Cook (1992) gave a general account of the development of faunal diversity. Environmental interpretation and estimates of extinction are made easier by the existence of snail-rich late Pleistocene and Holocene deposits spanning the last 300,000 years (Cook *et al.*, 1993), and by the application of amino-acid epimerization techniques to the dating of individual shells (Goodfriend, 1987, 1991; Goodfriend *et al.*, 1994).

THE ARCHIPELAGO AND ITS ENVIRONMENTAL HISTORY

Together with the Deserta Islands, Madeira (ca. 740 km²) and Porto Santo and its neighbouring islets (ca. 41 km²) constitute an archipelago of volcanic, oceanic origin. Madeira is mountainous, rising to over 1800 m, and contains a wide range of habitats and climatic zones, including subalpine regions, extensive laurel forests, and lower coastal areas with an approximately Mediterranean climate. Although some rocks are 15+ million years (MY) old, there have been more recent periods of volcanic activity, the last perhaps 0.75 MY ago (summary in Mitchell-Thomé, 1985). Substrata are almost exclusively volcanic in origin, and coasts are generally rocky and steeply shelving.

Only at the eastern extremity of the island are there soils of sea-sand origin on a low peninsula which is the driest part of the island. Ecologically, this peninsula now resembles parts of Porto Santo.

Porto Santo differs in many respects. One hill only rises just above 500 m; rocks are all dated to 12-14 MY old (Mitchell-Thomé, 1985), and with the exception of sea-cliffs to the northeast and some hill summits, the landscape is rounded, with sometimes massive colluvial deposits on hillsides. There is an extensive sandy beach along the southern coast, and sandy deposits cover most of the land below 100 m. They sometimes ascend higher, and the low center of the island is entirely covered by them, separating the rocky hills to the west and east. Rainfall is lower than on Madeira. No natural forest survives, and except for recent forestry plantations, the habitats available are heavily grazed grassland (often with bare, eroding sand) or a very open shrubby environment resembling Mediterranean garrique or phrygana.

Human occupation of the islands started in 1419-1420 A. D. Apart from widespread habitat destruction, there have been numerous deliberate and accidental introductions of plants and animals. Substantial areas of both islands are now dominated by non-native vegetation. There are no indigenous terrestrial mammals, but goats, sheep, rabbits, mice, and rats have all been introduced. There are many non-endemic mollusks, most of which have probably been introduced (Waldén, 1983; Goodfriend *et al.*, 1994), and these include Zonitidae with carnivorous habits.

Analysis of the stratigraphy and subfossil snails in the sandy deposits of Madeira demonstrates not only the locally catastrophic consequences of human disturbance and introductions (Goodfriend *et al.*, 1994) but also the occurrence of Pleistocene and pre-colonization environmental changes between more wooded (damp) and open (dry) landscapes. These sequences are interrupted by massive accumulations of fossil-free sand, indicating periods of dune mobility and (presumably) localized faunal extinctions (Cook *et al.*, 1993; Goodfriend *et al.*, 1996).

Analyses of the far more extensive deposits on Porto Santo are not yet complete, but it is clear that similar fluctuations occurred there, including drastic changes in lowland areas following human occupation. Unlike Madeira, Porto Santo is surrounded by a shelf of shallow water; sea-level depression in full glacial periods of the Pleistocene would not only have greatly increased the size of the island, but would also expose sand subsequently blown inland. Periods of dune mobility would isolate eastern and western hills (Cameron *et al.*, 1996).

MATERIAL

The land snail fauna of the archipelago has been

studied intensively since the 1820s, and Wollaston (1878) gave a remarkable and detailed account of the living and subfossil fauna then known. Many workers have studied the fauna in the second half of the twentieth century; Waldén (1983) provided an annotated checklist for the archipelago, to which later workers have made minor alterations and additions (Groh and Hemmen, 1984, 1986a, b; Hemmen and Groh, 1985; Holyoak and Seddon, 1986; Cook *et al.*, 1990; Seddon, 1990; Rähle, 1992).

In addition to work already published, we have drawn on data from our survey of laurel forests and coastal scrub in northern Madeira, and on a comprehensive survey of Porto Santo, the results of which will be published elsewhere. We thus have data on species diversity and occurrence from subfossil material, from good nineteenth century accounts, and from recent surveys which include detailed distributional data. Similar comprehensive surveys of the relatively inaccessible Deserta Islands have not been carried out, and we have not considered their fauna.

There are inevitable difficulties of taxonomic interpretation involved in such comparisons. We have chosen to ignore subspecific taxa, because early workers, including Wollaston, appear not to distinguish reliably between geographically replacing forms and varieties found at the same site. In general, we have accepted Waldén's (1983) nomenclature and assignments of taxonomic rank, with some adjustments made in the light of later work. Minor changes in assignment would make little difference to our conclusions. A list of species and their status is given in the Appendix.

There are also some difficulties in interpreting nineteenth century statements concerning abundance and distribution. Wollaston (1878), while generally meticulous, occasionally admitted to conflating samples from different localities, and sometimes appears to rely on distant memory. Contemporaries were often far less reliable. Twentieth century records are generally accurately localized.

DISTRIBUTION PATTERNS AND DIVERSITY

On both Madeira and Porto Santo, sample site diversities are modest, being mostly in the range of 5-15 species (Solem, 1984). While there are clear differences in habitat between some species, there is also evidence of geographical differentiation between faunas drawn from the same habitat (Cameron and Cook, 1992; Cook *et al.*, 1993; Cameron *et al.*, 1996).

The range of available habitats on Madeira is considerable. Faunas from laurel forests at mid- to high altitudes (500+ m) show little geographical variation, while those from drier environments at lower altitudes show much more. While not entirely consistent, these differences

can be attributed to climatic fluctuations which caused periodic isolation of fragments of dry, open, lowland habitats (Cook, in press).

The range of habitats is much more restricted on Porto Santo, and there are numerous cases of allopatric replacements of sibling species in similar environments (Fig. 1A). These are examples of non-adaptive radiation in the sense defined by Gittenberger (1991). While there are some habitat differences between species, most of the diversity is related to the isolation of hills caused by sand movement between them. The recent human disturbance has created a number of vicariant distributions (Fig. 1B): disjunct distributions which are known from Holocene subfossil material to have been continuous (Cameron *et al.*, 1996).

Geographical patterning is usually seen most clearly in Helicidae, which are in general far more abundant and diverse in open habitats than in the wetter and cooler laurel forests of Madeira. This is reflected in the greater number of helcid species (35) found alive on the overwhelmingly open and dry Porto Santo than on Madeira (30); the latter island is ca.18 times as large and has a far greater diversity of habitats.

EXTINCTIONS AND INTRODUCTIONS

We have two ways of estimating extinctions, the comparison of nineteenth and twentieth century records,

and a comparison of subfossil and recent records.

On Porto Santo, only one species, the massive helcid *Pseudocampylaea lowei*, appears to have become extinct in this century. Even in the nineteenth century it was known alive from one locality only (it is abundant as a subfossil, but no dates are available).

Our own survey of Porto Santo conducted over a three-week period in 1993 revealed all but two of the remaining species reliably identified by Wollaston, and these two have also been found recently (M. Seddon, pers. comm.).

Where Wollaston (1878) gave sufficient detail, most species appear to have maintained their distribution and abundance, but a few which were found in lowland, sandy areas appear to have retreated. Conversely, the introduced *Theba pisana* has expanded its distribution, now being found in nearly all locations with any sand in the soil.

The situation on Madeira is more complicated. A number of species cataloged by Wollaston were known from only one or a very few sites, and these are not always relocatable with certainty. The island has not been resurveyed at the intensity involved on Porto Santo.

Of the 80 endemic species recorded alive at any time described for Madeira, our recent surveys of eastern and northern Madeira have revealed 56. Of the 24 not recorded by us, five were unknown in the nineteenth century, nine have certainly been found by others in recent years, but ten appear not to have been found during this century

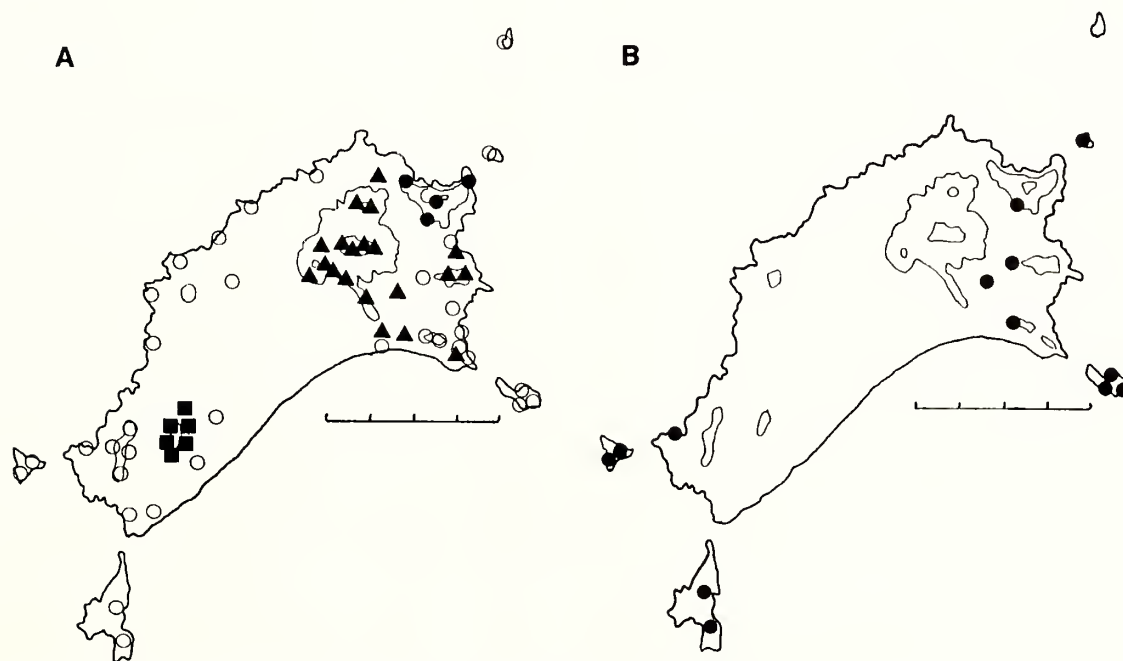


Fig. 1. Distributions of endemic species on Porto Santo. A. *Discula echinulata* (●), *D. bicarinata* (▲), and *D. leacockiana* (■). Other sites sampled shown as open circles. B. *Pseudocampylaea portosantana*. Contours shown at 200 and 400 m.

(Groombridge, 1992). Many of these ten were very localized in the nineteenth century; five of them belong to the genus *Leiostylis* - small and often cryptic. It is unlikely that all of them are genuinely extinct; we suggest that, at a maximum, ca.10% of endemic species known to Wollaston have died out in the last 120 years, and that all of them were very rare before that.

At least two species, *Actinella arridens* and *Janulus stephanophora*, appear to have become very much rarer in the last 100 years; no explanation occurs to us. The southwest of Madeira, subject to heavy disturbance, has not been surveyed in detail; other declines could have occurred there.

Despite this low overall extinction rate, some areas have clearly become impoverished. Sandy areas on both islands have depauperate endemic faunas, and high densities of the introduced *Theba pisana*. On Madeira, planted conifer forests are virtually devoid of snails (Cook *et al.*, 1972) and some other areas dominated by introduced mimosas are depauperate (Cook *et al.*, 1990). Conversely, some open country endemics, for example *Discula polymorpha* and *Actinella nitidiuscula*, appear to have colonized cleared areas with some success.

The good subfossil record enables us to estimate extinctions in another way. Table 1 shows the numbers of species known alive or only subfossil on both islands. The Helicidae are separated from other families for reasons given below. Taking both islands together, they have a higher apparent extinction rate than the other families ($\chi^2 = 5.54$, $p < 0.05$).

Interpretation, however, must take into account the chances of preservation in the deposits. Table 2 shows the proportions of species known in the fossil record which are now extinct, and the proportion of the total fauna known in subfossil condition. Helicidae are better represented in the deposits than other families, and a much higher proportion

Table 1. The numbers of species recorded alive at any time or found only as subfossils (extinct) in the endemic faunas of Madeira (a) and Porto Santo (b).

(a) Madeira			
	Helicidae	Other Families	Total
Living	30	50	80
Extinct	9	5	14
Total	39	55	94
% Extinct	23.1	9.1	14.9

(b) Porto Santo			
	Helicidae	Other Families	Total
Living	37	17	54
Extinct	12	3	15
Total	49	20	69
% Extinct	24.5	15.0	21.7

Table 2. The numbers of endemic species known in subfossil condition, their proportions of total faunas, and the extinction rate for species known as subfossils for Madeira (a) and Porto Santo (b).

(a) Madeira			
	Helicidae	Other Families	Total
Known Subfossil	22	20	42
% of all fauna	56.4	36.4	44.7
Extinct	9	5	14
% of Subfossil Extinct	40.9	25.0	33.3

(b) Porto Santo			
	Helicidae	Other Families	Total
Known Subfossil	43	11	54
% of all fauna	87.7	55.0	78.3
Extinct	12	3	15
% of Subfossil Extinct	27.9	25.0	27.8

of Porto-Santo than Madeiran species occur as subfossils. Fossiliferous deposits occur all over Porto Santo; they are confined to a small and atypical part of Madeira. The proportion of subfossil species now extinct is similar on both islands.

In the case of Madeira, of the 14 extinct species known from the sand deposits, at least nine appear to have died out after human colonization (Goodfriend *et al.*, 1994). We are not yet able to offer figures for Porto Santo.

The number and proportion of recent non-endemic species is much higher on Madeira than on Porto Santo (Table 3) and a lower proportion of non-endemics than endemics are Helicidae. Most non-endemics have probably been introduced (those which are anthropophilic almost certainly) but some, particularly very small species, could be native. Three non-endemics (*Punctum pygmaeum*, *Plagyrone placida*, and *Vitrea contracta*) are found as subfossils in pre-colonization deposits on Madeira, and *V. contracta* and *Balea perversa* have an exclusively montane distribution on Porto Santo. A small number of non-endemics also occur regularly in laurel forests. All slugs are non-endemic (Rähle, 1992).

DISCUSSION

THE EXTENT AND TIMING OF EXTINCTIONS

As estimated by changes over the last 100-150 yrs, the rate of apparent extinction reported here is very low for oceanic islands (Solem, 1990a; Groombridge, 1992) and especially for those subject to intense human intervention. The archipelago was discovered and colonized more than 400 yrs before detailed descriptions of the fauna were made. Early accounts (explored in Machado, 1947; Prestage, 1966; Crosby, 1986; and Ferraz, 1986) indicated large scale destruction of natural habitats by fire, fellings,

Table 3. The numbers of endemic and non-endemic species reported alive on both islands. Of Madeiran non-endemics, 13 are restricted anthrophiles. Figures in parentheses show the effect of excluding them.

(a) Madeira			
	Helicidae	Other Families	Total
Endemics	30	50	80
Non-Endemics	12 (6)	47 (40)	59 (46)
% Non-Endemics	28.6 (16.7)	48.5 (44.4)	42.4 (36.5)
Total	42 (36)	97 (90)	139 (126)

(b) Porto Santo			
	Helicidae	Other Families	Total
Endemics	37	17	54
Non-Endemics	14	8	12
% Non-Endemics	9.8	32.0	18.2
Total	41	25	66

and introduced mammals, and substantial agricultural exports were being made before the end of the fifteenth century. Extinctions could therefore have occurred on a large scale prior to nineteenth century surveys.

The subfossil record, which spans this period, suggests a higher rate of extinction of ca. 30% on both islands. The evidence from dating in the case of Madeira (Goodfriend *et al.*, 1994) suggests that two-thirds of this occurred after human occupation.

The record on Porto Santo is remarkably complete. Most parts of the island are sandy or near sand. Living species not found in deposits are mostly small rock-dwellers. Pending detailed analysis and dating, we can estimate that 20-25% of the fauna was destroyed by human colonization, but that it has since stabilized.

The record on Madeira is less complete, and could be unrepresentative of the island as a whole. Living faunas in the area of the deposits are poorer in endemics than many elsewhere (Cook *et al.*, 1990). On the other hand, the deposits have yielded nearly half the endemic species known from the island. An overall extinction rate similar to that on Porto Santo must be our best estimate.

Even these levels of post-colonization extinction are considerably lower than those recorded for the much shorter period of European colonization on many Pacific islands. These islands undoubtedly suffered earlier extinctions also, as a consequence of disturbance caused by the first human settlers.

CAUSES OF EXTINCTION

There is no direct evidence as to the causes of extinction, of the kind available for *Partula*, achatinellids, and endodontids on Pacific islands (Hadfield, 1986; Solem, 1990b; Cowie, 1992a). Some introduced Zonitidae and Subulinidae are potential predators, and introduced rodents certainly eat both native and introduced species, but we

cannot ascribe any extinctions to their presence.

There is likewise little evidence of competition between native and introduced species. Site diversities of endemic and non-endemic species are independent of one another (Cook, 1984) and non-endemics fill spaces in the shell size and shape distribution unoccupied by endemics (Cameron and Cook, 1989). In one instance, it is possible that competition has caused extinction: the extinct *Caseolus bowdichianus* was very abundant on sandy substrata on both islands before colonization. It has now been replaced by the introduced *Theba pisana* which is similarly abundant on sandy substrata (Goodfriend *et al.*, 1994).

Most of the indirect evidence we have points to habitat destruction as the primary cause of extinction. Human intervention caused instability in sand-based habitats, and these now have lower than average diversities on both islands (Cook *et al.*, 1990; Cameron *et al.*, 1996). On Madeira, regions dominated by planted conifers are nearly snail-free (Cook *et al.*, 1972), and areas dominated by other non-native vegetation are species-poor (Cook *et al.*, 1990).

DIVERSITY AND DURABILITY IN THE SURVIVING FAUNA

Both islands support numerous sites in which the fauna is dominated by endemic and native species, at diversity levels (5-20 species) which are not depauperate by world standards (Solem, 1984). On Porto Santo, site diversities in rocky habitats are almost identical to those reported for similar maquis and phrygana habitats in the Aegean region (Cameron *et al.*, unpub.).

Thus while there is evidence of damage, and indeed of extinctions, the present state of the archipelago's fauna appears to be much healthier than that in many other oceanic islands subject to extensive human intervention.

Comparison with accounts of extinctions in these other islands suggests that there could be significance in the fact that many Madeiran and Porto Santan species have evolved to live in rather dry, rocky, and open environments, rather than being arboreal or dependent on damp litter from native trees. Not only did this preadapt them to resist clearance, it is also these habitats which have been subject to the greatest fluctuations in size and continuity before human colonization, building up allopatric diversity, and tolerance of change.

It is also the case that substantial areas of native laurel forests survive on the northern side of Madeira. Where native forests survive on some Pacific islands, high levels of extinction have followed the introduction of molluscan, arthropod, and vertebrate predators (Solem, 1990b; Cowie, 1992b). Introduced predators have not had this effect here (see above), nor in the Gulf of Guinea (Gascoigne, 1994), where *Euglandina rosea* (Férussac,

1818), the introduced predatory snail which has devastated many Pacific island faunas, has not been introduced.

In general, the pattern seen on Madeira resembles that found in the Mediterranean region, where despite massive and prolonged human alterations of the environment, many natives (and some restricted endemics) have survived, with the addition of species spread by humans and associated with their activities (Mylonas, 1984). The Madeiran fauna is clearly of European rather than African origin (Waldén, 1983) and the same family, the Helicidae, dominates the faunas of both the archipelago and of southern Europe. Many species are adapted to rather dry, exposed environments.

This apparent durability does not justify complacency over conservation. Destruction of the habitats on one small hill on Porto Santo (an area of less than 0.5 km²) would eliminate three endemic species, and the destruction of remaining laurel forest on Madeira would remove far more.

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LITERATURE CITED

- Cameron, R. A. D. and L. M. Cook. 1989. Shell size and shape in Madeiran land snails: do niches remain unfilled? *Biological Journal of the Linnean Society* 36:79-96.
- Cameron, R. A. D. and L. M. Cook. 1992. The development of diversity in the land snail fauna of the Madeiran archipelago. *Biological Journal of the Linnean Society* 46:105-114.
- Cameron, R. A. D., L. M. Cook, and J. Hallows. 1996. Land snails on Porto Santo: adaptive and non-adaptive radiation. *Philosophical Transactions of the Royal Society of London, B* 351:309-327.
- Clarke, B. and J. Murray. 1969. Ecological genetics and speciation in land snails of the genus *Partula*. *Biological Journal of the Linnean Society* 1:31-42.
- Cook, L. M. 1984. The distribution of land molluscs in eastern Madeira and the Desertas. In: *World Wide Snails*, A. Solem and A. C. van Bruggen, eds. pp. 46-55. Brill, Leiden.
- Cook, L. M. In press. Madeiran landsnails: habitat, isolation and evolution. *Biological Journal of the Linnean Society*.
- Cook, L. M., R. A. D. Cameron, and L. A. Lace. 1990. Land snails of eastern Madeira: speciation persistence and colonization. *Proceedings of the Royal Society of London, B* 239:35-79.
- Cook, L. M., G. A. Goodfriend, and R. A. D. Cameron. 1993. Changes in the land snail fauna of eastern Madeira during the Quaternary. *Philosophical Transactions of the Royal Society of London, B* 339:83-103.
- Cook, L. M., T. Jack, and C. W. A. Pettitt. 1972. The distribution of land molluscs in the Madeiran archipelago. *Boletim do Museu municipal, Funchal* 26:5-30.
- Cowie, R. H. 1992a. Evolution and extinction of Partulidae, endemic Pacific land snails. *Philosophical Transactions of the Royal Society of London, B* 335:167-191.
- Cowie, R. H., ed. 1992b. The impact of alien species on island ecosystems: extended abstracts of a symposium, 30 May 1991, Honolulu, Hawaii, XVII Pacific Science Congress. *Pacific Science* 46:383-404.
- Crosby, A. W. 1986. *Ecological Imperialism: The Biological Expansion of Europe, 900-1900*. Cambridge University Press, Cambridge. 380 pp.
- Ferraz, M. de L. de Freitas. 1986. *A Ilha de Madeira sob o Dominio de Casa Senhorial do Infante D. Henrique e seus descendentes*. Região Autonomia da Madeira, Funchal. 79 pp.
- Gascoigne, A. 1994. The biogeography of land snails in the islands of the Gulf of Guinea. *Biodiversity and Conservation* 3:784-807.
- Gittenberger, E. 1991. What about non-adaptive radiation? *Biological Journal of the Linnean Society* 43:263-272.
- Goodfriend, G. A. 1987. Evaluation of amino acid racemization/epimerization dating using radiocarbon-dated fossil land snail shells. *Geology* 15:698-700.
- Goodfriend, G. A. 1991. Patterns of racemization and epimerization of amino acids in land snail shells over the course of the Holocene. *Geochimica et Cosmochimica Acta* 55:293-302.
- Goodfriend, G. A., R. A. D. Cameron, and L. M. Cook. 1994. Fossil evidence of recent human impact on the land snail fauna of Madeira. *Journal of Biogeography* 21:309-320.
- Goodfriend, G. A., R. A. D. Cameron, L. M. Cook, M. A. Courty, N. Federoff, A. Kaufman, E. Livett, and J. Tallis. 1996. The Quaternary eolian sequence of Madeira: stratigraphy, chronology and paleoenvironmental interpretation. *Palaeogeography, Palaeoclimatology and Palaeoecology* 120:195-234.
- Groh, K. and J. Hemmen. 1984. Revision der Gattung *Boettgeria* O. Boettger 1863. *Archiv für Molluskenkunde* 116:183-217.
- Groh, K. and J. Hemmen. 1986a. Zur Kenntnis der Vitriniden des Madeira-Archipels (Pulmonata, Vitrinidae). *Archiv für Molluskenkunde* 115:1-39.
- Groh, K. and J. Hemmen. 1986b. *Geomitra (Serratorotula) gerberi* n. subgen. n. sp. aus dem Quaternär von Porto Santo (Pulmonata: Helicidae). *Archiv für Molluskenkunde* 117:33-38.
- Groombridge, B., ed. 1992. *Global Biodiversity: Status of the Earth's Living Resources*. Chapman and Hall, London. 585 pp.
- Hadfield, M. G. 1986. Extinction in Hawaiian achatinelline snails. *Malacologia* 27:67-81.
- Hemmen, J. and K. Groh. 1985. Eine neue Art der Gattung *Geomitra* Swainson auf Porto Santo (Pulmonata: Helicidae). *Archiv für Molluskenkunde* 116:73-80.
- Holyoak, D. T. and M. B. Seddon. 1986. An undescribed *Leiostylia* (Gastropoda: Pupillidae) from Madeira. *Journal of Conchology* 31:191-193.
- Machado, J. F., ed. 1947. *Descobrimento da Ilha da Madeira e discurso da Vida e Feitos dos Capitães da dita Ilha (Jeronimo Dias Leite, 1579)*. University of Coimbra, Coimbra, Portugal. 137 pp.
- Mitchell-Thomé, R. C. 1985. Radiometric studies in macaronesia. *Boletim Museu municipal, Funchal* 37:52-85.
- Mylonas, M. 1984. The influence of man: a special problem in the study of the zoogeography of terrestrial molluscs on the Aegean Islands, Greece. In: *World Wide Snails*, A. Solem and A. C. van Bruggen, eds. pp. 249-260. Brill, Leiden.
- Prestage, E. 1966. *The Portuguese Pioneers*. Black, London. 352 pp.
- Rähle, W. 1992. Nacktschnecken (Arionidae, Milacidae, Agriolimacidae und Limacidae) von Madeira und Porto Santo (Mittelatlantische Inseln). *Malacologische Abhandlungen Staatliches Museum für Tierkunde, Dresden* 16:13-24.
- Seddon, M. B. 1990. Undescribed Quaternary land-snail species from S. W. Porto Santo (Madeiran Islands) (Mollusca: Gastropoda).

- Journal of Conchology* 33:299-304.
- Solem, A., 1983. *Endodontoid Land Snails from Pacific Islands (Mollusca: Pulmonata: Sigmurethra). Part II. Families Punctidae and Charopidae, Zoogeography*. Field Museum of Natural History, Chicago. 336 pp.
- Solem, A. 1984. A world model of land snail diversity and abundance. In: *World Wide Snails*, A. Solem and A. C. van Bruggen, eds. pp. 6-22. Brill, Leiden.
- Solem, A. 1990a. Limitations of equilibrium theory in relation to land snails. *Atti dei Congressi Lincei* 85:97-116.
- Solem, A. 1990b. How many Hawaiian land snails are left? and what we can do for them. *Bishop Museum Occasional Papers* 30:27-40.
- Tomiyama, K. and T. Kurozumi. 1992. [Terrestrial mollusks and conservation of their environment in the Ogasawara Islands.] *Regional Views* 5:39-81. (In Japanese with English summary)
- Waldén, H. W. 1983. Systematic and biogeographical studies of the terrestrial gastropods of Madeira, with an annotated check-list. *Annales Zoologici Fennici* 20:265-275.
- Wollaston, T. V. 1878. *Testacea Atlantica*. Reeve, London. 588 pp.
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APPENDIX

Three lists are given here: (a) species known only in subfossil condition, (b) endemic species recorded alive at some time, and (c) non-endemic species recorded alive. There are, inevitably, cases of taxonomic uncertainty and of difficulties in interpreting the status of records. Minor disagreements in categorization do not affect our general conclusions, and so we have not annotated the lists, which should not be regarded as definitive accounts of the fauna.

(a) Species known only as subfossils, presumed extinct (all endemic).

Madeira

Helicidae:

Geomitra delphinula (Lowe, 1831)
G. watsoni (Johnson, 1897)
Caseolus bowdichianus (Férussac, 1832)
C. sphaerulus (Lowe, 1854)
C. abjectus (Lowe, 1831)
C. subcalliferus (Lowe in Pfeiffer, 1859)
Actinella arcinella (Lowe, 1854)
A. promontoriensis Walden, 1983

Others:

Leiostylia wollastoni (Paiva, 1866)
Amphorella grabhami (Pilsbry, 1908)
Cylichnidia cylichna (Lowe, 1852)
Boettgeria lorenziana Groh and Hemmen, 1984
Phenacolimax crassus Groh and Hemmen, 1986

Porto Santo

Helicidae:

Geomitra gerberi Groh and Hemmen, 1986
G. acarinata Hemmen and Groh, 1985
Caseolus bowdichianus (Férussac, 1832)
C. baixoensis Walden, 1983
Actinella morenensis Seddon, 1990
A. crassiuscula (Cockerell, 1922)
A. arcinella (Lowe, 1854)
Spirorbula latinea (Paiva, 1866)
Discula echinoderma (Wollaston, 1878)
D. cockerelli (Noronha, 1923)
Leptaxis chrysomela (Pfeiffer, 1846)
L. psammophora (Lowe, 1852)

Others:

Craspedopoma mucronatum (Lowe, 1830)
Leiostylia espigaoensis Seddon, 1990
L. subcorneocostata Seddon, 1990

(continued)

Appendix (continued)

(b) Endemic species found alive. (*, also found as subfossils; +, not found alive in twentieth century).

Madeira

Helicidae:

- **Heterostoma paupercula* (Lowe, 1831)
- **Geomitra tiarella* (Webb and Berthelot, 1833)
- G. moniziana* (Paiva, 1867)
- +*G. delphinuloides* (Lowe, 1860)
- Spirorbula latens* (Lowe, 1852)
- **S. squalida* (Lowe, 1852)
- **Caseolus compactus* (Lowe, 1831)
- C. leptostictus* (Lowe, 1831)
- Disculella compar* Lowe, 1831
- D. spirulina* Cockerell, 1921
- Actinella lentiginosa* (Lowe, 1831)
- **A. actinophora* (Lowe, 1831)
- A. arcta* (Lowe, 1831)
- A. fausta* (Lowe, 1831)
- A. carinofausta* Walden, 19983
- A. robusta* (Wollaston in Pilsbry, 1894)
- A. arridens* (Lowe, 1831)
- **A. obserata* (Lowe, 1854)
- A. armitageana* Lowe, 1854
- **A. nitiduscula* (Sowerby, 1824)
- A. giramica* (Lowe, 1852)
- A. anaglyptica* (Reeve, 1852)
- **Leminiscia calva* (Lowe, 1831)
- +*L. galeata* (Lowe, 1860)
- **Discula polymorpha* (Lowe, 1831)
- **Leptaxis erubescens* (Lowe, 1831)
- **L. furva* (Lowe, 1831)
- **L. membranacea* (Lowe, 1852)
- **L. undata* (Lowe, 1831)

Others:

- Craspedopoma neritoides* (Lowe, 1860)
- **C. mucronatum* (Lowe, 1830)
- C. lyonnetaum* (Lowe, 1852)
- C. monizianum* (Lowe, 1860)
- **C. trochoideum* (Lowe, 1860)
- Columella microspora* (Lowe, 1852)
- **Truncatellina linearis* (Lowe, 1852)
- **Stauroidon saxicola* (Lowe, 1852)
- Leiostyla cheillogona* (Lowe, 1831)
- L. vineta* (Lowe, 1852)
- L. irrigua* (Lowe, 1852)
- L. loweana* (Wollaston, 1878)
- +*L. cassidula* (Lowe, 1852)
- L. concinna* (Lowe, 1852)
- **L. laurinea* (Lowe, 1852)
- **L. sphinctostoma* (Lowe, 1831)
- L. arborea* (Lowe, 1854)
- L. simulator* (Pilsbry, 1923)
- L. fusca* (Lowe, 1852)
- +*L. laevigata* (Lowe, 1852)
- L. recta* (Wollaston, 1878)
- **L. millegrana* (Lowe, 1852)
- +*L. abbreviata* (Lowe, 1852)
- **L. cassida* (Lowe, 1831)
- +*L. lamellosa* (Lowe, 1852)
- +*L. gibba* (Lowe, 1852)

Porto Santo

Helicidae:

- **Heterostoma paupercula* (Lowe, 1831)
- **Geomitra coronata* (Deshayes in Férussac, 1819)
- **Spirorbula oblecta* (Lowe, 1831)
- **S. depauperata* (Lowe, 1831)
- **Caseolus compactus* (Lowe, 1831)
- **C. consors* (Lowe, 1831)
- **C. commixtus* (Lowe, 1854)
- **C. sphaerulus* (Lowe, 1854)
- **C. abjectus* (Lowe, 1831)
- **C. subcalliferus* (Lowe in Pfeiffer, 1859)
- **C. calculus* (Lowe, 1854)
- **C. hartungi* (Albers, 1852)
- **C. punctulatus* (Sowerby, 1824)
- **C. solidus* (Lowe, 1831)
- **Actinella effugiens* Walden, 1983
- Lemniscia michaudi* (Deshayes, 1831)
- **Discula bicarinata* (Sowerby, 1824)
- D. echinulata* (Lowe, 1831)
- **D. leacockiana* (Wollaston, 1878)
- **D. oxytropis* (Lowe, 1831)
- D. turricula* (Lowe, 1831)
- **D. cheiranticola* (Lowe, 1831)
- **D. calcigena* (Lowe, 1831)
- **D. tectiformis* (Wood, 1828)
- D. albersi* Lowe, 1852
- **D. bulverii* (Wood, 1828)
- **D. rotula* (Lowe, 1831)
- **D. pulvinata* (Lowe, 1831)
- **D. attrita* (Lowe, 1852)
- **D. testudinalis* (Lowe, 1852)
- Leptaxis erubescens* (Lowe, 1831)
- **L. wollastoni* (Lowe, 1852)
- **L. nivosa* (Sowerby, 1824)
- **Pseudocampylea portosanctana* (Sowerby, 1824)
- +*P. lowei* (Férussac, 1835)
- **Lampadia webbiana* (Lowe, 1831)
- **Helix subplicata* Sowerby, 1825

Others:

- **Leiostyla corneocostata* (Wollaston, 1878)
- L. relevata* (Wollaston, 1878)
- L. ferraria* (Lowe, 1852)
- L. degenerata* (Wollaston, 1878)
- L. monticola* (Lowe, 1831)
- **L. calathiscus* (Lowe, 1831)
- Eucobresia media* (Lowe, 1854)
- **Cecilioides eulima* (Lowe, 1854)
- **Amphorella melampoides* (Lowe, 1831)
- **A. triticea* (Lowe, 1854)
- **A. oryzae* (Lowe, 1852)
- A. tuberculata* (Lowe, 1852)
- A. cimensis* Walden, 1983
- A. gracilis* (Lowe, 1831)
- A. terebella* (Lowe, 1852)
- **Cyllichnidia ovuliformis* (Lowe, 1831)
- Boettgeria lowei* (Albers, 1852)

(continued)

Appendix (continued)

L. filicum Holyoak and Seddon, 1986
Lauria fanalensis (Lowe, 1852)
Hemilauria limneana (Lowe, 1852)
 +*Discus guerinianus* (Lowe, 1852)
 +*D. defloratus* (Lowe, 1854)
Phenacolinax nitidus (Gould, 1848)
 **P. marcidus* (Gould, 1848)
P. riuvensis (Lowe, 1831)
P. behnii (Lowe, 1851)
*P. albopalliatu*s Groh and Hemmen, 1986
 **Janulus bifrons* (Lowe, 1831)
 **J. stephanophora* (Deshayes, 1835)
 +*Cecilioides eulima* (Lowe, 1854)
Amphorella tornatellina (Lowe, 1831)
 **A. cf. minor* (Wollaston, 1878)
A. mitriformis (Lowe, 1852)
A. producta (Lowe, 1852)
A. iridescens (Wollaston, 1878)
Pyrgella leacockiana (Lowe, 1852)
Boettgeria deltostoma (Lowe, 1831)
B. depauperata (Lowe, 1854)
*B. obesi*uscula (Lowe, 1863)
B. exigua (Lowe, 1831)
B. crispa (Lowe, 1831)

(c) Non-endemic species (all recorded alive). (* = very restricted or strictly anthropophile).

Madeira

Helicidae:

**Candidula intersecta* (Poirét, 1801)
 **Cernuella virgata* (da Costa, 1778)
C. vestita (Rambur, 1868)
 **Helicella conspurcata* (Draparnaud, 1801)
Cochlicella acuta (Müller, 1774)
C. barbara (Linné, 1758)
Caracollina lenticula (Michaud, 1831)
Theba pisana (Müller, 1774)
 **Otala lactea* (Müller, 1774)
 **Cepaea nemoralis* (Linné, 1758)
Helix aspersa Müller, 1774

Others:

Carychium tridentatum (Risso, 1826)
C. minimum Müller, 1774
Cochlicopa lubrica (Müller, 1774)
C. lubricella (Porro, 1838)
Columella aspera Walden, 1966
Vertigo pygmaea (Draparnaud, 1801)
Lauria cylindracea (da Costa, 1778)
Discocharopa aperta (Moellendorff, 1888)
Vallonia costata (Müller, 1774)
V. pulchella (Müller, 1774)
V. excentrica Sterki, 1893
Acanthinula aculeata (Müller, 1774)
Plagyrona placida (Shuttleworth, 1852)
Punctum pygmaeum (Draparnaud, 1801)
Toltecia pusilla (Lowe, 1831)
Helicodiscus singleyanus (Pilsbry, 1890)
 **Discus rotundatus* (Müller, 1776)
 **Hawaiiia minuscula* (Binney, 1840)

Porto Santo

Helicidae:

Cochlicella acuta (Müller, 1774)
C. barbara (Linné, 1758)
Caracollina lenticula (Michaud, 1831)
Theba pisana (Müller, 1774)

Others:

Vitrea contracta (Westerlund, 1871)
Cecilioides acicula (Müller, 1774)
Rumina decollata (Linné, 1758)
Balea perversa (Linné, 1758)
Oxychilus alliarius (J. S. Müller, 1822)
Testacella maugei Férussac, 1819
Milax gagates (Draparnaud, 1801)
Lehmannia valentiana (Férussac, 1823)

(continued)

Appendix (continued)

- Vitrea contracta* (Westerlund, 1871)
Nesovitrea hammonis (Stroem, 1765)
Oxychilus draparnaudi (Beck, 1837)
O. alliarius (J. S. Miller, 1822)
**O. helveticus* (Blum, 1881)
Zonitoides arboreus (Say, 1816)
**Z. nitidus* (Müller, 1774)
Euconulus fulvus (Müller, 1774)
Cecilioides acicula (Müller, 1774)
C. nyctelia (Bourguignat, 1856)
Ferussacia folliculus (Gronovius, 1781)
Subulina striatella (Rang, 1831)
Rumina decollata (Linné, 1758)
Testacella maugei Férussac, 1819
**T. haliotideae* Draparnaud, 1801
Arion lusitanicus Mabilie, 1868
A. hortensis Férussac, 1819
A. intermedius (Normand, 1852)
A. pascalinus Mabilie, 1868
Milax gagates (Draparnaud, 1801)
**M. sowerbyi* (Férussac, 1823)
Deroceras laeve (Müller, 1774)
D. panormitanum (Lessona and Pollonera, 1882)
D. lombricoides (Simroth, 1891)
D. reticulatum (Müller, 1774)
Lehmannia valentiana (Férussac, 1823)
Limax flavus Linné, 1758
L. maximus (Linné, 1758)